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HETEROSIS IN BARLEY

BY

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF GENETICS

EDMONTON, ALBERTA

JULY, 1963

UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read,
and recommend to the Faculty of Graduate Studies for
acceptance, a thesis entitled "Heterosis in Barley"
submitted by Tefvik Fikret Demirkan in partial fulfilment
of the requirements for the degree of Master of Science.

ABSTRACT

A six-parent diallel cross of barley (15 F_1 hybrids plus 6 selfs) was used in the study of heterosis involving the characters, number of tillers per plant, days-to-head, days-to-flower, top weight per plant, root weight per plant, spike (rachis) length, grain yield, plant height and its subcharacters, number of internodes per stem, length of internodes, length of the pedunculum.

The results for most of the characters were analysed graphically as a diallel set on an array basis, followed by more detailed graphical and computational treatment of individual crosses.

The tillering in most hybrids, as compared with the corresponding parents, was more rapid and intensive during the first 45 days of growth. The final counts at the flowering and maturity time, however, revealed an opposite trend. Consequently, although positive heterotic effects were present, a change in direction did in some cases have a neutralizing tendency. Days-to-head and days-to-flower appear to be closely related thus suggesting that the same genes or closely-linked genes are responsible for these characters. Although the characters top weight and root weight are phenotypically positively correlated ($r = 0.615^*$), there is a negative correlation regarding the potence ratios. The heterotic effects present for these characters operate in opposite directions. The character spike (rachis) length is inherited as a dominant and, in a few cases, as an overdominant (heterotic) trait, mainly in a positive direction.

For the character grain yield, the dominance in most hybrids is transgressive (heterotic) and in all cases toward the higher expression.

Plant height is inherited mostly as a transgressive (heterotic) trait in a positive direction, although its component subcharacters in some cases show an opposite trend.

ACKNOWLEDGEMENT

The writer wishes to express his sincere thanks and appreciation to Dr. L.P.V. Johnson for his guidance, supervision during the course of the project and for his assistance in preparation of this manuscript.

Sincere thanks are also expressed to Dr. R. Aksel for his advice, encouragement and guidance in the presentation of the results, to the National Research Council of Canada for financial assistance and to the University of Alberta for the opportunity of carrying out these studies.

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". . . Heterosis is a ubiquitous phenomenon. That it may be due to different mechanisms in different organisms appears to be axiomatic. Certainly, heterosis in corn, where selection has acted on the heterozygote over a great period of time, might be expected to stem from different causes than heterosis in a diploid, self-pollinated crop such as barley. . . ."

J.E. Grafius (1959)

I. INTRODUCTION

Heterosis, because of its immense value in plant and animal breeding, and of its evolutionary significance in natural populations, has occupied for many years an important position in genetics. Hundreds of papers have been contributed toward the elusive genetic explanation of this phenomenon.

In recent years one of the chief interests in general breeding work has been in the utilization of heterosis. The outstanding example in this field is hybrid maize. With self-pollinating crops, the practical importance is less clear, and it is doubtful whether fixable heterosis, as a general phenomenon exists in inbreeding species; and also, whether hybridity per se has any advantage over the pure line regarding the higher expressivity of its character.

In the present work an attempt has been made to throw some additional light on the mode of inheritance of some quantitative characters in barley by using the diallel-cross technique as well as by scaling tests of individual crosses. The results may assist in determining the relative importance of heterosis in self-fertilizing crops, such as barley.

II. LITERATURE REVIEW

There are relatively few studies of heterosis in cultivated self-fertilizing species, such as wheat, oats and barley.

Rosenquist (20) found certain wheat hybrids to be very superior when spaced four inches apart but intermediate to the parental types when spaced at one inch intervals. Until further evidence is produced it would seem better to assume that in certain crosses the hybrids inherit a single gene, or a complex of genes, which controls their reactions to some limiting factor or group of factors. Thus the hybrids might be expected to show the same general relative growth rate as one parent at least through part of the growth cycle without it being necessary to suppose so complex a character as the growth rate to be determined by a single gene.

The effect of "artificial selfing," was investigated by Griffie (8) in his work on heterosis of wheat. He found that the emasculation operation gave smaller grains.

Engledow and Pal (6) working in reciprocal crosses of wheat found small differences established in the F_1 with identical vigour in F_2 and F_3 . Also measuring the respiration rate of germinating grains they indicated further evidence against the possibility that embryo weight influences hybrid vigour in wheat.

Coffman and Davis (3); Coffman and Wiebe (4) worked on heterosis in oats. They have found increase in kernel weight, in plant height and panicle length, in weight of total plant straw and grain of F_1 's.

Barley was studied by Engledow and Pal (6) who did not find any marked differences between parents and F_1 .

Immer (13), in analysing heterosis for the complex character yield of grain, studied the obvious components, such as tillering, number of kernels per ear, and weight of seed. He found significant superiority in yield of grain for F_1 crosses between varieties of barley, with reduction in yield during successive generations of natural selfing in the same material.

Suneson and Riddle (22), using a male-sterile mutant, were able to obtain large numbers of F_1 plants of barley without the artificial manipulations of emasculation and pollination, obtaining sufficient material for a valid comparison between F_1 and parents. On an average they found that the F_1 was about 20% higher than the mean of the parents in yield of grain; but that it was superior to the best of the parents only in three out of seven combinations studied.

Engledow and Pal (6) do not state definitely whether they have used emasculation and artificial pollination in obtaining the seed of the parents used in comparisons between these and F_1 in barley. They also studied the effect of artificially selfing six varieties. The artificially selfed seed germinated more rapidly than the seed from normal selfing, but after 40 days there was no evident difference between the plants from the two types of seed.

Powers (18), Hagberg (11) found that heterosis in, e.g., grain yield, depends upon combination of favourable dominance in the component characters: "combination heterosis."

Coffman and Wiebe (4); Engledow and Pal (6); Immer (13) compared F_1 with F_2 and F_3 in some self fertilizing species, but they made no comparisons between the inbreeding curves for different characters or combinations.

Hagberg (11) used barley parents emasculated and artificially pollinated, simulating the crosses. Seed setting was the same in the parents and crosses. He concluded that in regard to rapid development, earliness, tillering, length of ear and yield, most of the F_1 combinations were intermediate or equal to the best parent.

Powers (13) has shown that in a cross between Hordeum deficiens and Hordeum vulgare the F_1 , which is two-row barley, gave a greater yield of seed per plant than either the two-row or six-row parents. Thus weight of seed per plant showed heterosis.

Williams and Gilbert (23) working on tomato, concluded that the greater part of the average heterosis for yield in this material is due simply to the relative distribution of the levels of the components of yield in the parents of a given cross.

Grafius (9) discussed the heterosis on the bases of the geometrical model for yield where yield is the volume of a rectangular parallel piped with edges representing heads per plant, seeds per head

and average seed weight. He suggested that there are no genes for yield per se, but only genes for components of yield. According to him the F_1 vigor of yield in barley is due to epistasis.

III. MATERIALS AND METHODS

Six different varieties of 6-rowed barley (Hordeum vulgare) were crossed in all combinations without reciprocals, giving a total of fifteen crosses: $C_n^r = \frac{6!}{(6-2)! 2!} = 15$. These varieties are as

as follows:

Atsel (A)

Bonneville (B)

Edda (E)

Frontier (F)

Husky (H)

Montcalm (M)

The crosses were made in the greenhouse in 1961. The experimental material, consisting of six parents and their fifteen crosses, was seeded in pots. The pots were completely randomized in two growth chambers each of which was considered as one replicate. The soil used was California mixture (U.C. Soil Mix C Fertil. II (C)) its composition for one cubic yard being as follows:

50% sand

50% peat

120 grams potassium nitrate

120 grams potassium sulfate

1125 grams super phosphate (single) (18 - 20% P_2O_5)

1172 grams calcium carbonate hydrate

780 grams magnesium carbonate

1125 grams Hoof and horn

Two growth chambers were maintained as closely as possible under identical conditions regarding the temperature, humidity and duration of light. Temperature was maintained at 70° F. for 7 days, 55° F. for 13 days, 60° F. for 14 days, and for the remaining time at 70° F. Humidity was regulated automatically in accordance with the temperature. An equal amount of water was given to each pot. Duration of light was adjusted according to the day lengths to which spring-sown varieties are subject under normal field conditions in Edmonton. In two replications 336 plants were used.

The illumination periods in the growth chambers and number of days after sowing were as follows:

Hours of illumination		Days after seeding	
<u>Hours</u>	<u>Minutes</u>	<u>Days</u>	<u>Total</u>
16	00	7	7
16	15	13	20
16	35	10	30
16	50	10	40
17	00	10	50
16	50	10	60
16	35	13	73
16	15	remaining days	

During the course of the experiment, observations and measurements were made on the following characters:

(a) Through the growing period

1. Number of tillers at specified times
2. Number and lengths of internodes in first tillers
3. Time of heading
4. Time of flowering

(b) At maturity

1. Length of internodes
2. Height of three longest tillers
3. Weight of top of plants
4. Weight of root
5. Yield

In order to avoid the effect of differential seed size on the expression of the characters under study, the seed sizes of the parental varieties was adjusted to that of the corresponding F_1 seed by weighing each seed separately. There was no difference between the parents and their crosses respecting the size of seeds sown.

Twenty-five days after seeding the number of tillers was counted. The time of heading, when the awns extruded from the sheath, was recorded on string tags, and the time of flowering was considered to coincide with the extrusion of the anthers first from the florets.

At maturity, before harvesting, height of the three longest tillers was measured from the soil level to the top of the spike.

The internodes of the main tillers of the plants were counted and measured (in mm.) in order to obtain data relative to heterosis. After harvesting the plants were cut from the pots and kept in the envelopes till threshing. After weighing the top of the plants with kernels, grains were weighed separately to obtain the yield for each plant. The roots of the plants from each pot were washed and weighed after drying.

After collecting the data, graphical diallel cross analyses (Hayman, (12); Aksel and Johnson, (1)) were made on most of the characters in order to have a general idea regarding the dominance relationship of the parents. This analysis was followed by the calculation of the heritable fixable components of variation (d) and heritable non-fixable components of variation (h) from the parents and their F_1 offspring. The calculations were performed on each cross separately. The following formulas were used:

$$S^2 = \frac{n_1 S_1^2 + n_2 S_2^2 + \dots + n_k S_k^2}{(n_1 + n_2 + \dots + n_k) - k} \quad (1)$$

S^2 being the pooled variance, $S_1^2, S_2^2, \dots, S_k^2$ the variances observed within the parents and crosses and n_1, n_2, \dots, n_k the corresponding numbers of observations.

$$(d) = \frac{1}{2} (\bar{x}_{Pi} - \bar{x}_{Pj}) \quad (2)$$

where \bar{x}_p terms are the mean measurements (or counts as the case may be) of the two parents. The corresponding standard errors were found as:

$$\pm S_d = \frac{1}{2} \sqrt{S^2 \left(\frac{1}{n_i} + \frac{1}{n_j} \right)} \quad (3)$$

where $i = 1, 2, \dots, k$; $j = 1, 2, \dots, k$.

$$(h) = \bar{x}_{(F_{ij})} - \frac{1}{2} (\bar{x}_{Pi} + \bar{x}_{Pj}) \quad (4)$$

and the corresponding standard errors

$$\pm S_h = \sqrt{s^2 \left(1 + \frac{1}{4n_i} + \frac{1}{4n_j} \right)} \quad (5)$$

(Snedecor, (21); Cochran and Cox, (5)).

IV. EXPERIMENTAL RESULTS

1. Number of tillers

The average values for the character, number of tillers per plant, at specified times, are given in Table 1, and presented graphically in Fig. 1 and Fig. 2.

Table 1. Average numbers of tillers at specified times and stages

Plants	<u>Days after seeding</u>			At flowering	At harvesting
	25	35	45		
A	2.31	6.06	7.66	12.26	13.53
B	2.18	5.53	9.00	12.20	14.20
E	3.80	8.66	13.40	16.26	17.66
F	2.75	6.26	11.13	14.46	16.66
H	2.73	6.20	9.46	11.56	12.33
M	2.93	5.86	8.46	12.93	14.53
A × B	2.69	7.15	11.84	13.00	13.53
A × E	2.63	7.73	11.93	13.13	13.53
A × F	3.00	8.40	11.93	15.26	15.93
A × H	3.46	8.46	9.53	11.66	13.53
A × M	3.00	7.13	8.66	12.13	12.73
B × E	2.64	6.28	8.07	9.78	10.20
B × F	2.93	7.66	11.80	12.33	12.32
B × H	2.73	6.80	8.26	10.46	10.60
B × M	2.80	6.46	8.06	11.26	11.86
E × F	3.26	7.26	8.80	10.66	10.80
E × H	3.13	8.26	11.80	13.00	13.73
E × M	2.78	7.28	10.71	12.14	12.50
F × H	3.06	6.73	8.26	9.06	9.13
F × M	2.53	6.26	7.60	9.20	5.60
H × M	2.80	7.26	9.80	13.06	13.60

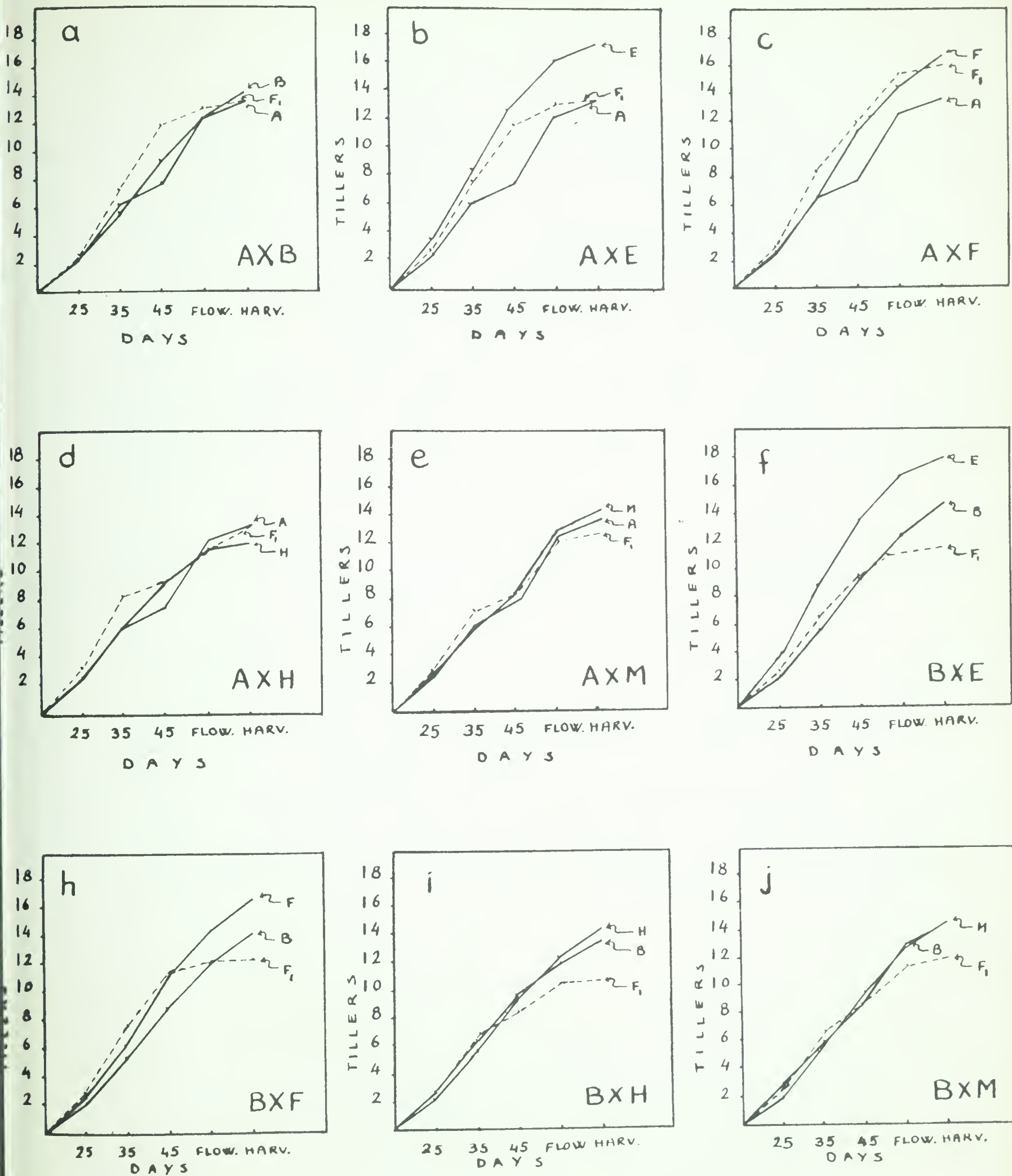


Fig. 1. At specified times, number of tillers of parents and F₁ barley hybrids.



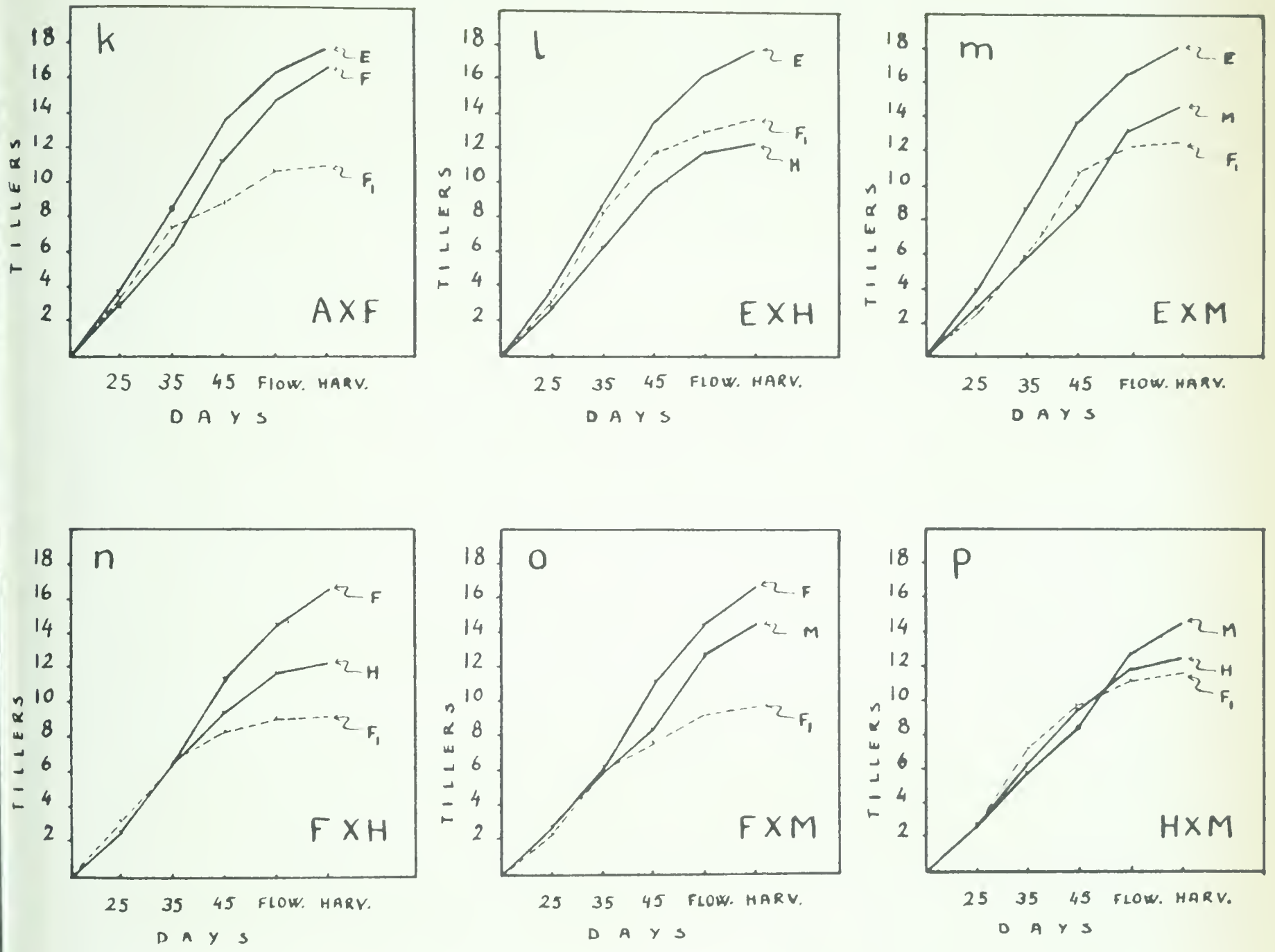


Fig. 2. At specified times, number of tillers of parents and F₁ barley hybrids.

The graphical treatment shows that in the crosses $A \times B$, $A \times F$, $A \times H$, $A \times M$, $B \times F$, and $H \times M$ the numbers of tillers per plant, on the average, are higher in the crosses than in their corresponding parents during the first 45 days; but the numbers drop to intermediate or equal to one of the parents, or even lower than the lowest parent, at the flowering time (e.g., cross $B \times F$). In the remaining crosses ($A \times E$, $B \times E$, $B \times H$, $B \times M$, $A \times F$, $E \times H$, $E \times M$, $F \times H$, $F \times M$) the expression of this character seems to be rather intermediate during the first period of 45 days, after which it follows the same pattern as in the previous crosses. It may be said, consequently, that heterosis is present during the first stages but disappears with the approach of flowering time, indicating that in most of the hybrids the period between seeding and flowering is marked by more intensive expression of growth rate and tiller formation in the hybrid as compared to the corresponding parents. It is interesting to note that at flowering time in 10 out of 15 crosses the number of tillers is less than in the parents. This indicates that in these hybrids tiller formation is earlier and lower in number than in the parents, thus giving a more uniform heading and ripening of F_1 plants.

Diallel cross graphical analysis

Since the crosses were made in a diallel cross pattern graphical analysis of the data was used as a preliminary genetic survey of the situation. This analysis was performed by simple plotting of the W_r , V_r points of intercept. The procedure was followed for most of the metrical characters considered.

2. Days to heading

As revealed by the graph Fig. 3 all the W_r , V_r points of intercepts lie to the right of the line of unit slope passing through the origin. This indicates the presence of heterosis in nearly all arrays. The intercepts of A and M points suggest complete dominance; whereas the other points, arranged about the regression line (more or less parallel to the line of unit slope and passing well below the origin) show fairly strong overdominance, or heterosis.

The detailed picture of the individual crosses and their respective parents is given in Fig. 7A. It is clear that the transgressions (heterotic effects) are toward the earliness in most of the crosses (especially in the $B \times E$, $B \times F$, $B \times H$, $B \times M$, $E \times F$, $E \times H$, $E \times M$, $F \times H$, $F \times M$).

3. Days to flowering

In Fig. 4, the W_r , V_r points of intercepts also lie to the right of the line of unit slope through the origin. Heterosis is present in all arrays. Actually, the scattering of the points of intercept is similar to that of heading time. This may be due to the fact that the two characters are controlled by the same genes or by closely linked genes.

4. Top weight per plant

The order of dominance of the parents regarding the character top weight (i.e., the total of organic mass produced above the soil level) is F, M, H, B, E and A as illustrated by the W_r , V_r

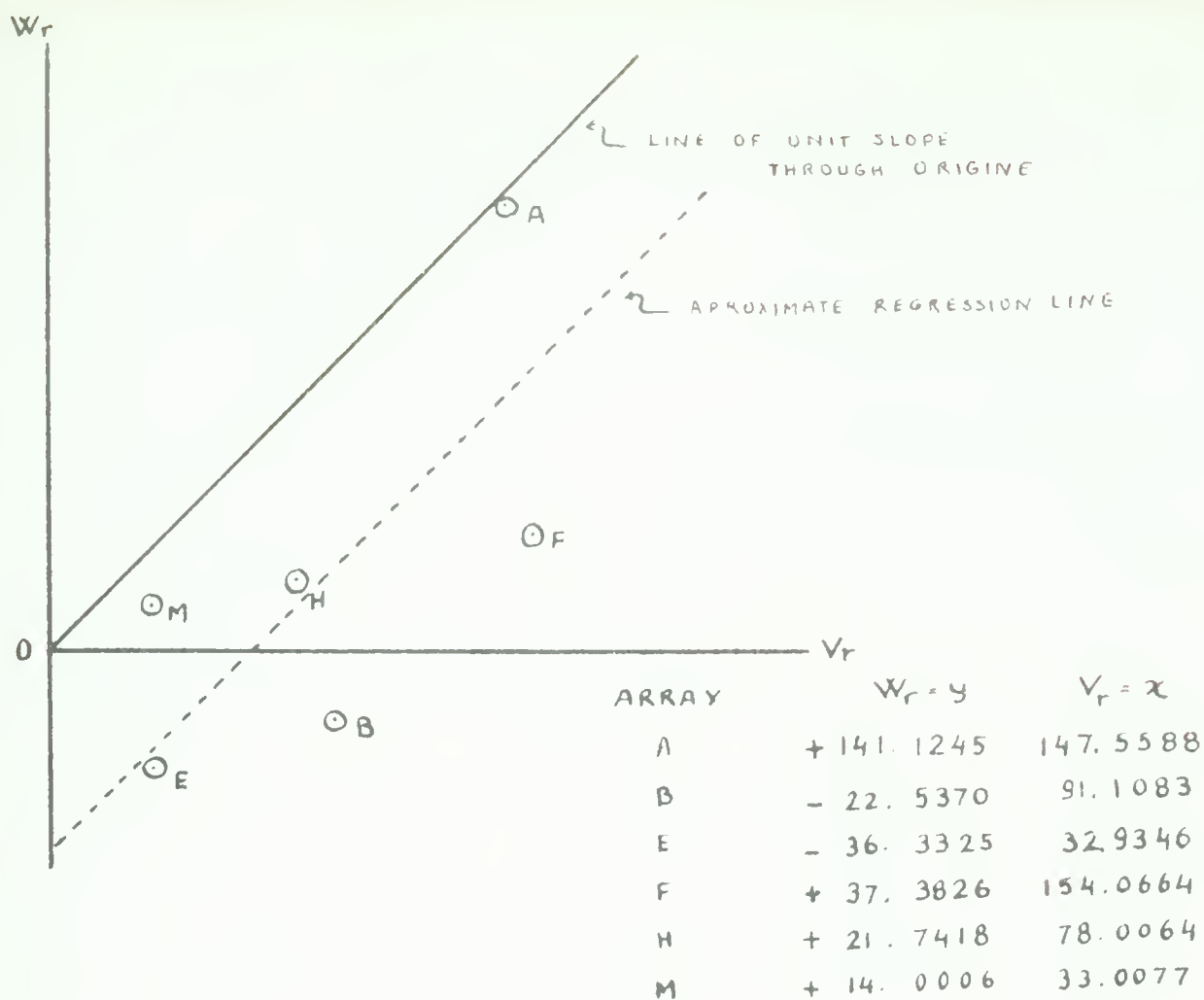


Fig. 3. Days to heading W_r , V_r graph.

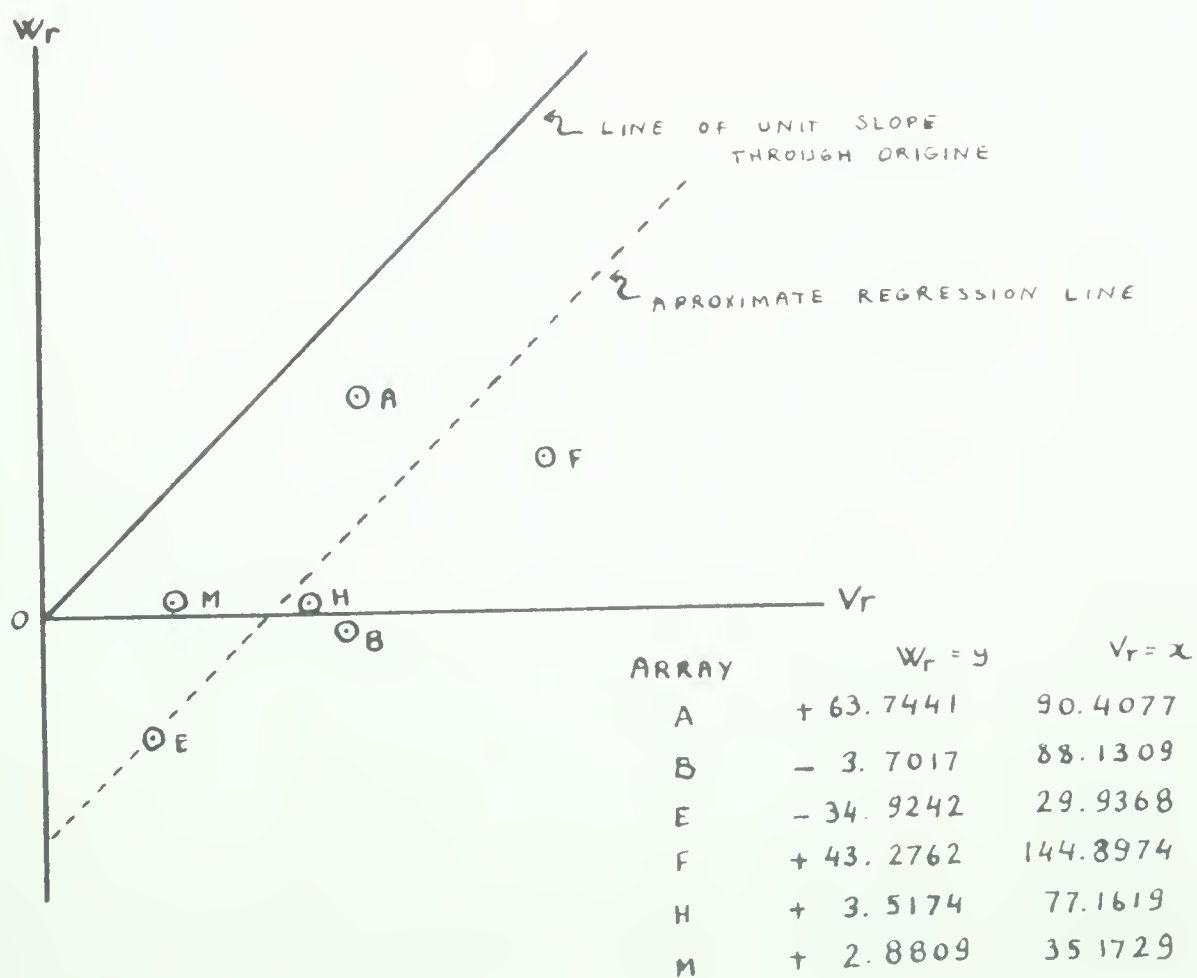


Fig. 4. Days to flowering W_r , V_r graph.



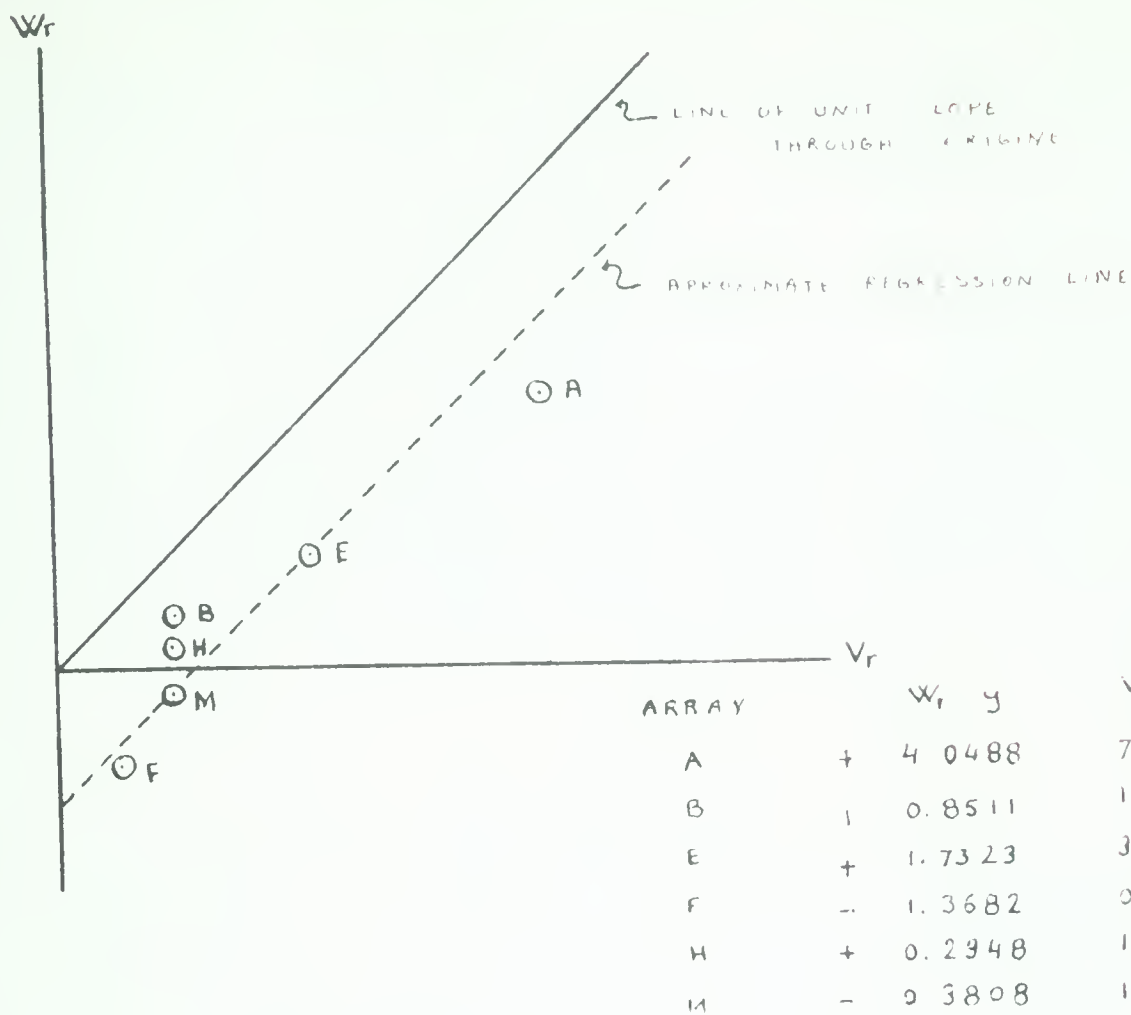


Fig. 5. Top weight per plant W_r , V_r graph.

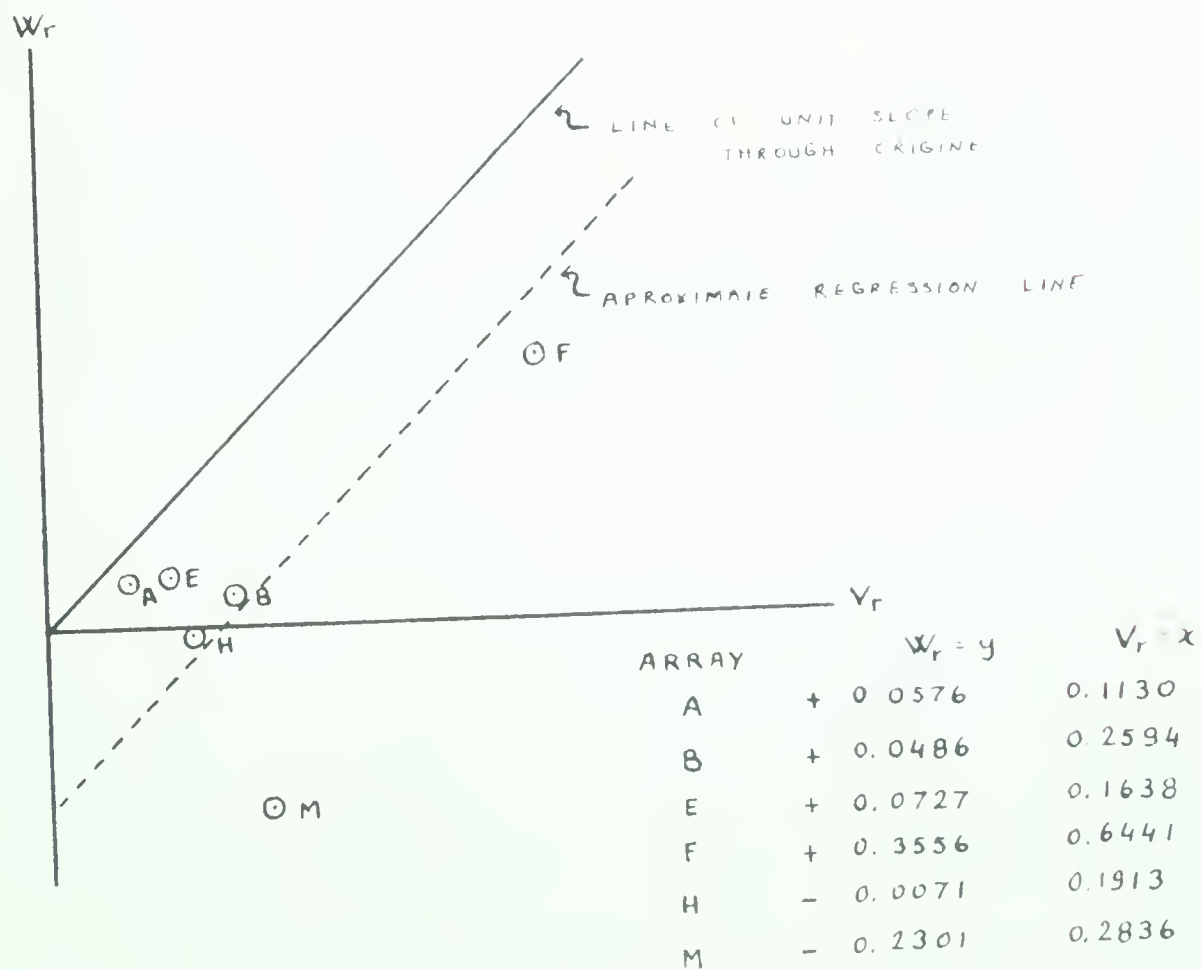


Fig. 6. Root weight per plant W_r , V_r graph.

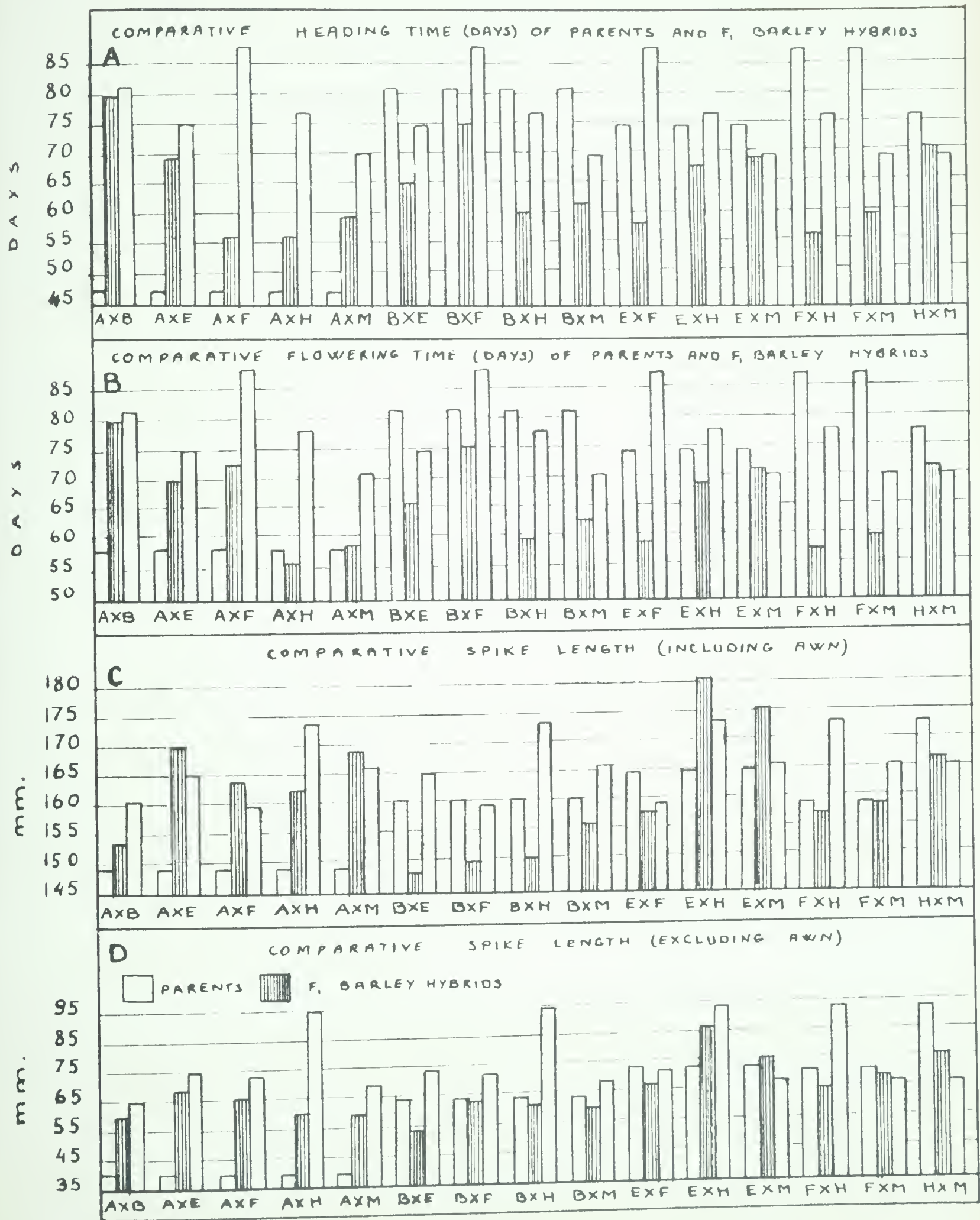


Fig. 7. Comparison of F₁ hybrids with their parents for heading time (A), flowering time (B), spike length (C), (D).

graph of Fig. 5. From the same graph it is seen that on the average there is overdominance or heterosis in all six arrays. The situation of individual crosses is given in Fig. 8B. As illustrated in this figure, pronounced heterosis is present in the crosses, A x E, A x F, A x H, B x E, B x F, B x H, E x F, E x H, E x M, F x H and H x M, the transgression being toward higher expression of the character. In the remaining crosses there is complete dominance in the same direction (cross A x B) or no dominance, i.e. additive effect of the genes by which the parents differ among themselves (crosses A x H, B x M and F x M).

5. Root weights per plant

Regarding this character, the situation appears to be more or less similar to that for the top weight, with the main difference that the W_r , V_r points of intercept for A and F exchanged their places, Fig. 6. The detailed analysis of Fig. 8D, however, shows that the heterotical transgressions are mainly in the direction of the lower expression of the character (see crosses B x E, B x F, B x H, B x M, E x F, E x H, F x H and F x M), whereas the dominance in the remaining crosses is toward both the lower and the higher expression of the character.

The standardized deviation graph, Fig. 9, Johnson, L.P.V. and Aksel, R. (15) of the potence ratio (h/d) where

$$h = x_F - \frac{1}{2} (P_1 + P_2) \text{ and}$$

$$d = \frac{1}{2} (P_1 - P_2) \quad \text{Mather (16)}$$

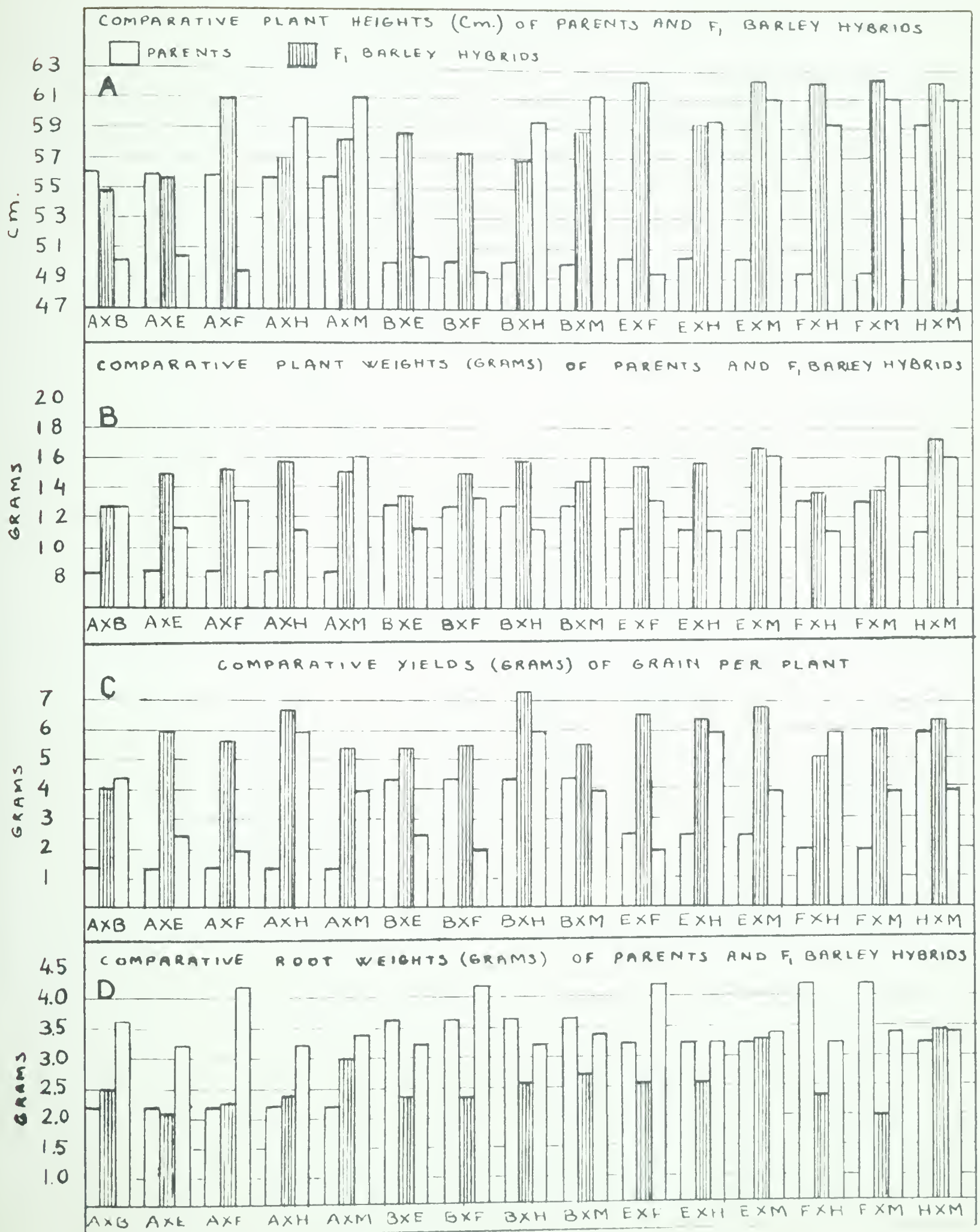
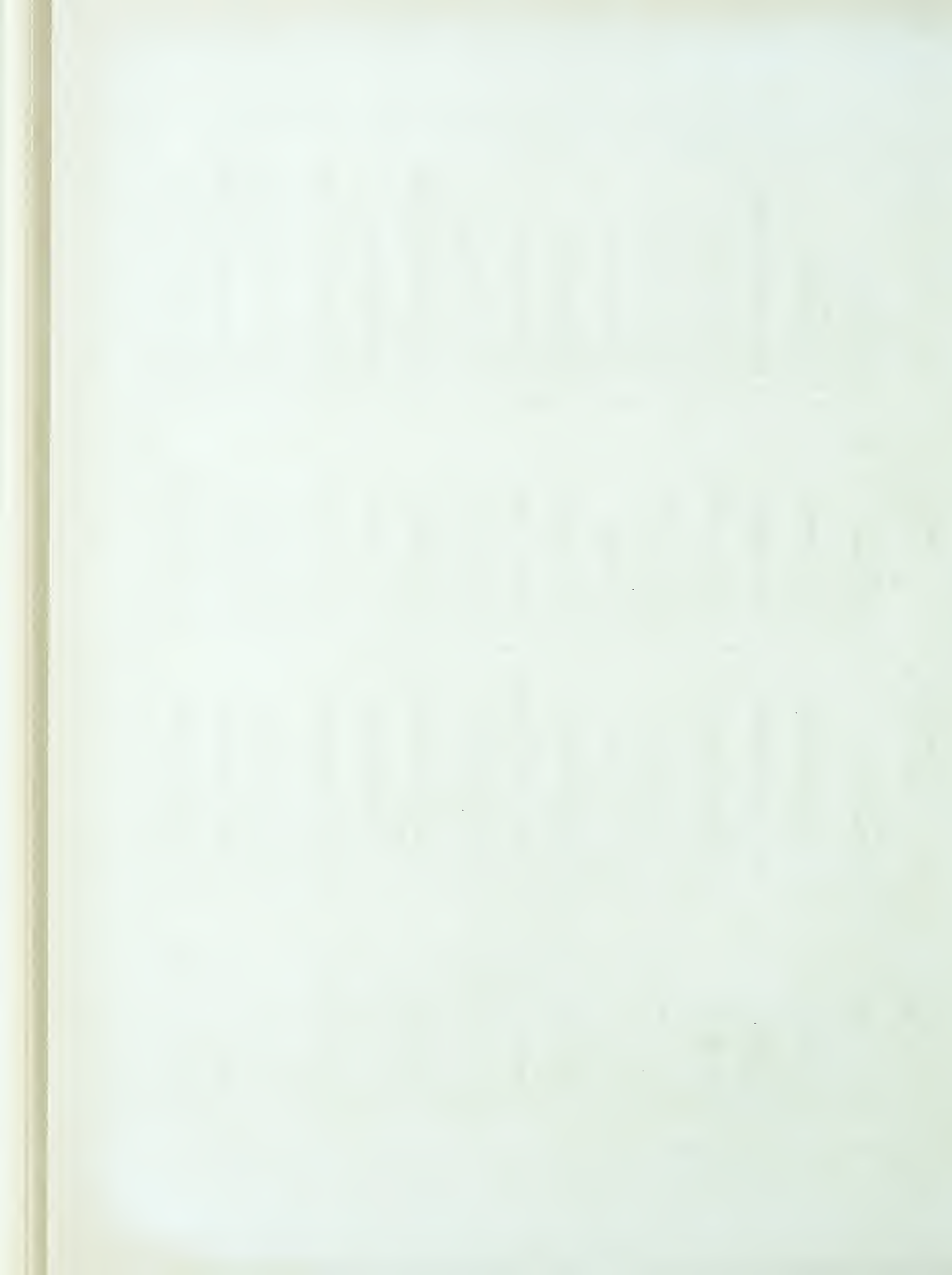


Fig. 3. Comparisons of F₁ hybrids with their parents for plant height (A), plant weight (B), yield (C), root weight (D).



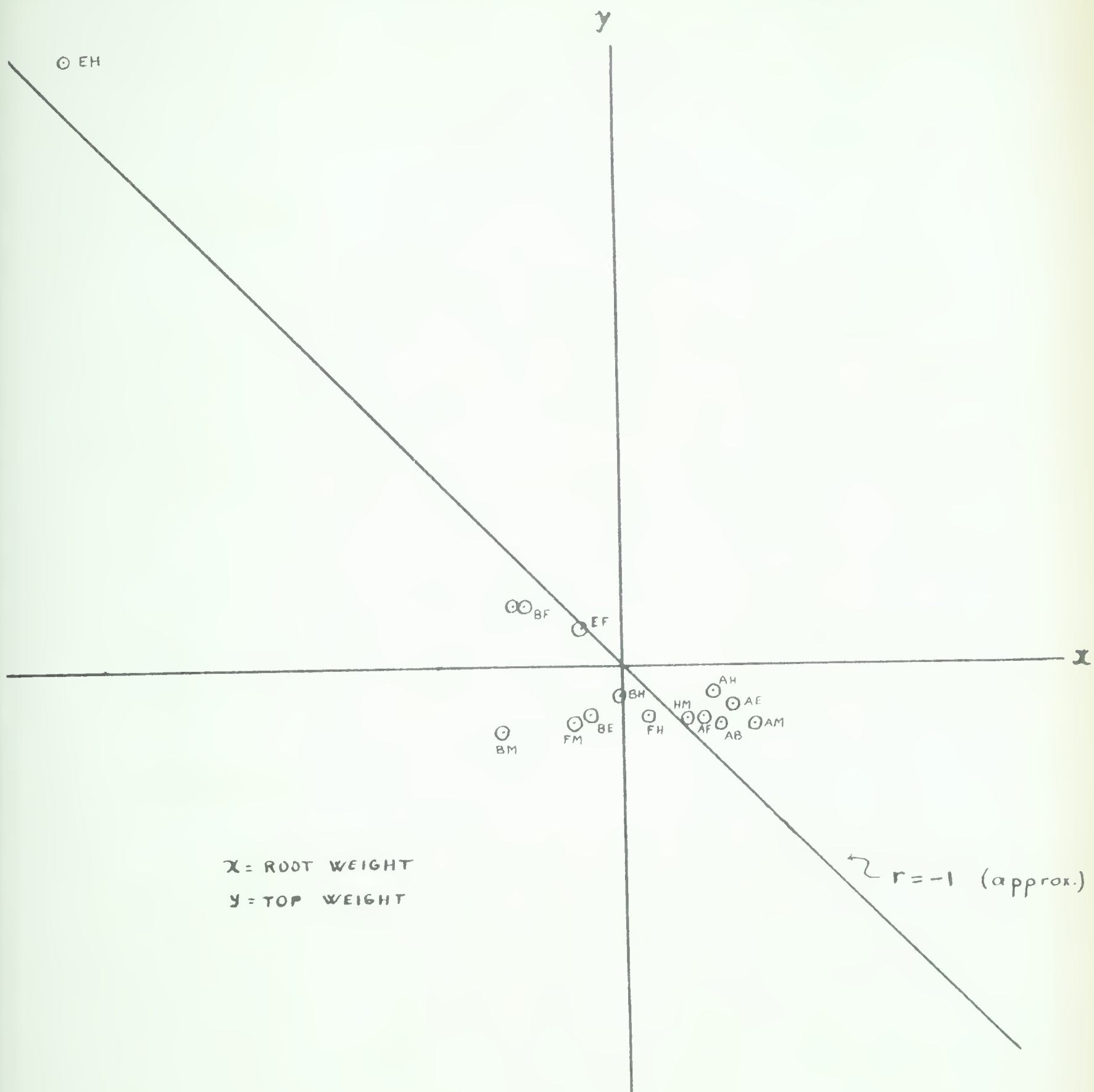


Fig. 9. Standardized deviations graph $(h/d)_{x_i} : (h/d)_{y_i}$
 $(h/d)_{x_i}$ = potence ratio for character root weight;
 $(h/d)_{y_i}$ = potence ratio for character top yield.
 $i = 1, 2, \dots, 15.$

shows that the direction of dominance in its different degrees, as already mentioned, is opposed in the two characters. The degree of correlation between the characters root weight and top weight is very pronounced and has a negative value ($r = -1$, approx.).

6. Spike length

As seen in the graph of Fig. 10, W_r , V_r points of A and M lie on the left of the line of unit slope through the origin, which means that, on the average, the dominance is partial regarding the dominance relationship in individual crosses. Fig. 7D shows that dominance is partial in the crosses $A \times B$, $A \times E$, $A \times F$, $A \times M$ and $E \times H$, complete in cross $B \times F$, and that in the crosses $B \times E$, $B \times F$, $B \times H$, $B \times M$, $E \times F$, $E \times M$, $F \times H$ some transgression is present. In the remaining crosses genic interaction seems to be of an additive nature. Somewhat the same situation may be seen in Fig. 7C.

7. Grain yield

Regarding yield, heterosis seems to be present in most of the crosses, since all the W_r , V_r points of intercept are on (array B) or below and to the right of the line of unit slope through the origin, Fig. 11. The performance of individual crosses is illustrated in the graph Fig. 8C. From this graph it may be seen that marked transgressions are present in the crosses $A \times E$, $A \times F$, $A \times H$, $A \times M$, $B \times E$, $B \times F$, $B \times H$, $B \times M$, $E \times F$, $E \times M$ and $F \times M$. Complete dominance may be assumed to be present in the remaining crosses.

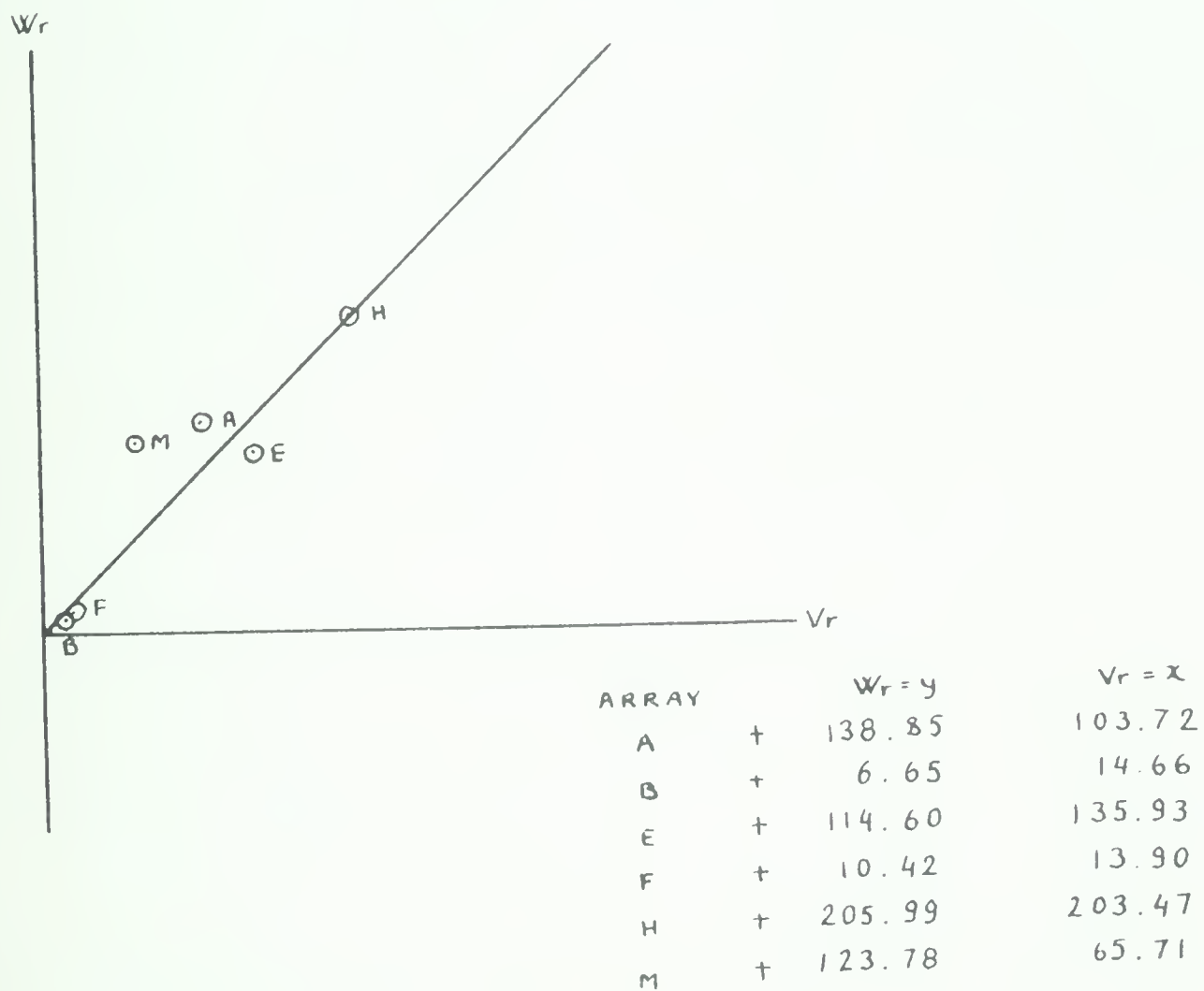


Fig. 10. Spike (rachis) length W_r , V_r graph.



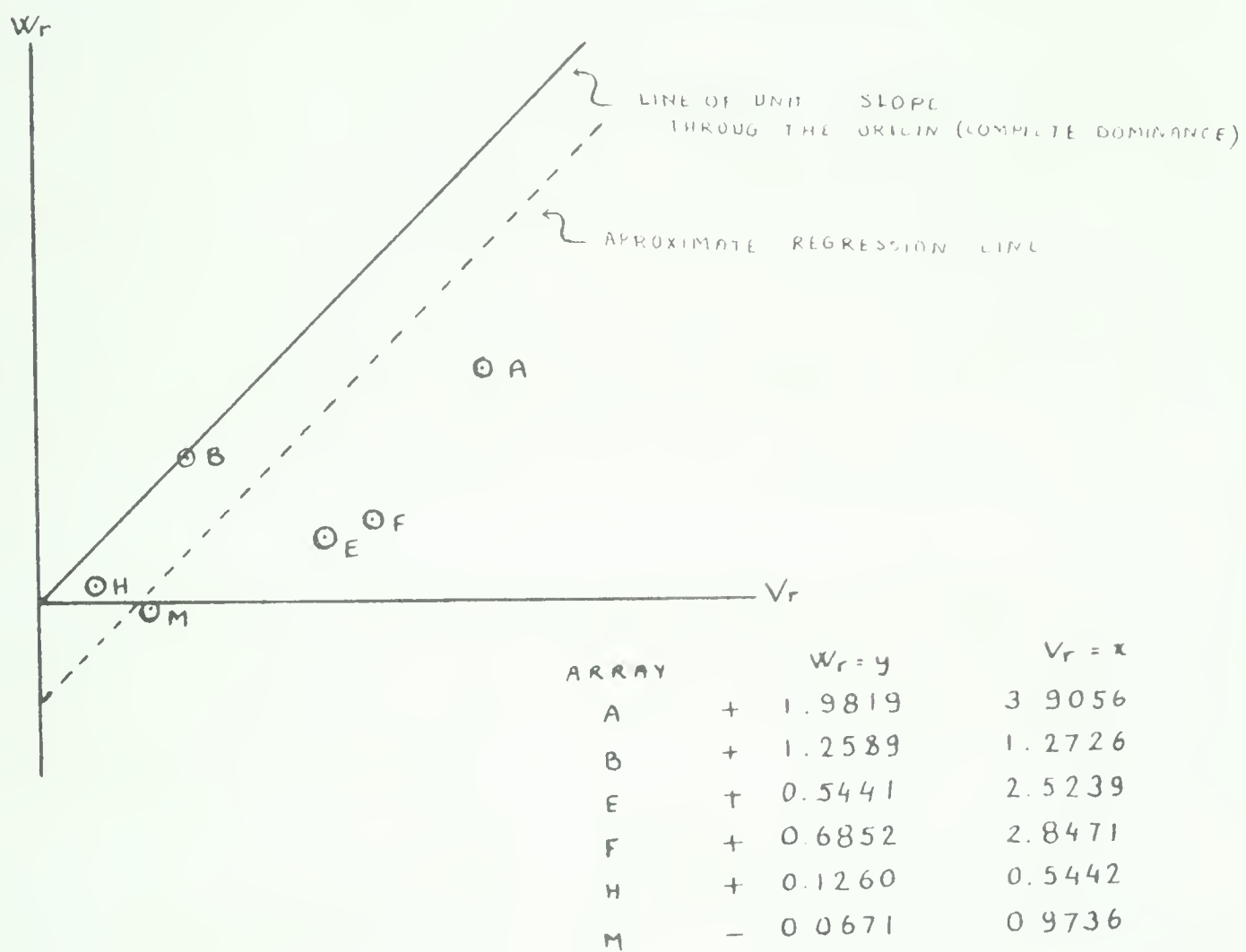


Fig. 11. Grain yield W_r , V_r graph.



8. Plant height

Analysis of plant height (in mm.) was based on measurements of the three main tillers of each plant.

Since all the W_r , V_r points of intercept lie to the right of the line of unit slope, overdominance or heterosis is indicated in all arrays (Fig. 12). Although only approximately drawn, the regression line is more or less parallel to the line of unit slope denoting the lack of nonallelic interaction (on the average). Some nonallelic interaction, however, may be present in E and F. The order of the parents for plant height is as follows: A, H, B, E and F.

With 15 crosses and 6 parents, the total number of degrees of freedom to be used in calculating the pooled error variance is $N - 21$, where

$$N = n_A + n_B + n_{AB} + \dots + n_{HM}.$$

Consequently,

$$S^2 = \sum x_i S_i^2 / (N - 21); i = A, B, AB, \dots, HM, \text{ and}$$

$$\text{having } \sum_{i=1}^{21} \frac{n_{ij} S_{ij}^2}{ij} = 3,526,635.3779, \text{ thus}$$

$$N - 21 = 827 - 21 = 806, \text{ and}$$

$$S^2 = 4375.4780$$

The necessary data for the calculation of S^2 are listed in Table 2.

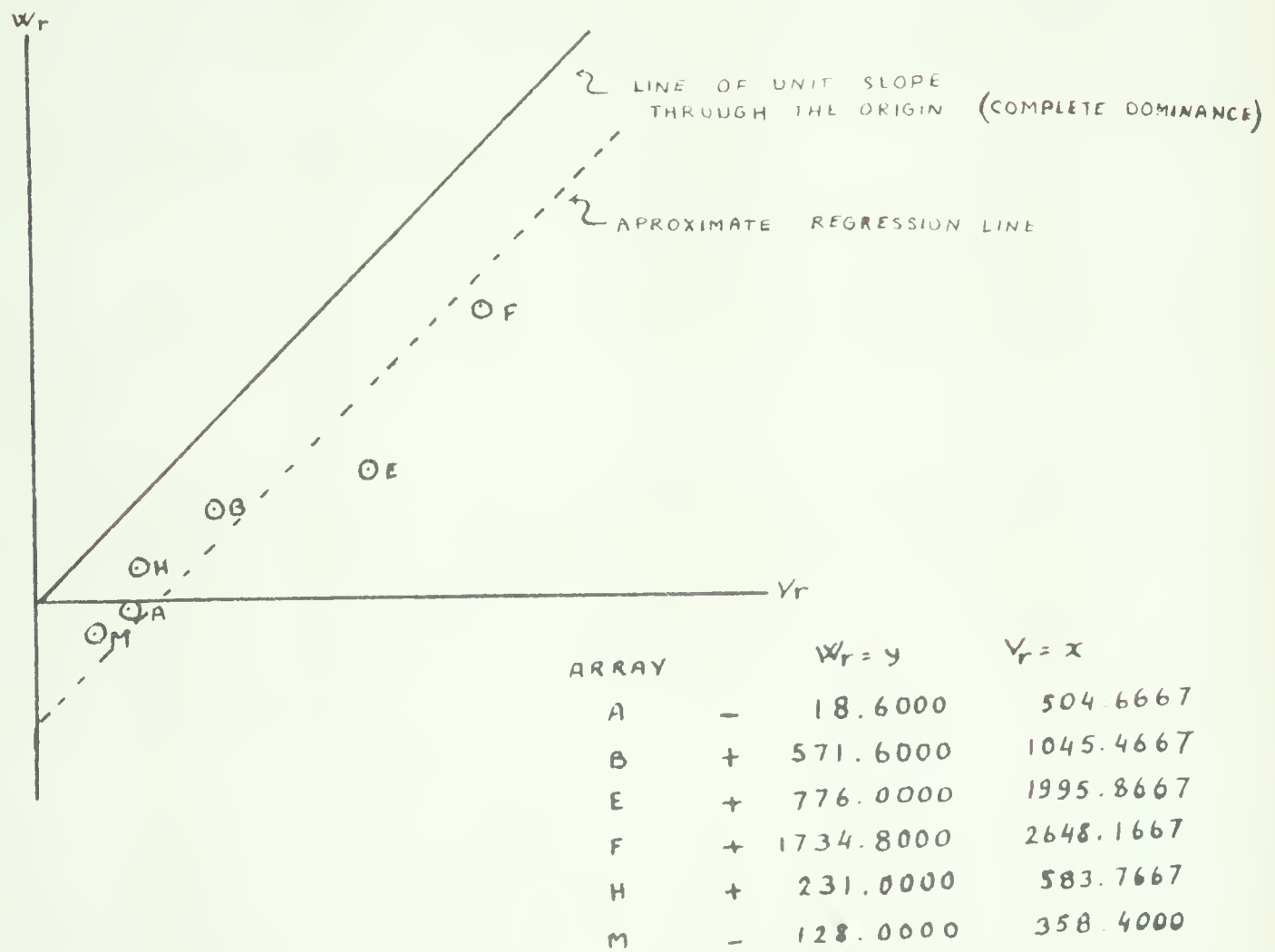


Fig. 12. Plant height W_r , V_r graph.



Table 2. The numbers, variances and means relating to individual parental varieties and crosses

Variety x cross	n_{ij}	s^2_{ij}	\bar{x}_{ij}
A	39	2559.1447	558.59
B	36	10036.8851	501.53
E	42	3993.3365	503.93
F	40	4746.4102	493.50
H	42	4575.3097	594.76
M	37	5851.6167	610.68
AxB	36	4771.5885	546.11
A xE	42	2766.1585	557.50
A xF	42	2651.3707	609.05
A xH	39	3195.4473	565.77
A xM	39	4323.4157	580.51
B xE	39	2803.6789	585.51
B xF	39	4684.6578	571.67
B xH	36	2475.9342	368.19
B xM	39	3415.1157	588.20
E xF	39	2662.0789	620.64
E xH	40	4844.8567	593.62
E xM	39	3710.3684	622.44
F xH	42	3611.7560	620.95
F xM	39	5607.1052	625.38
H xM	41	6820.5750	620.54
Sum	827		
$i = A, B, AB, \dots HM, 21$			
$j = A, B, AB, \dots HM, 21$			

From the data presented in Table 2, and by using the appropriate formulas as given in Section III, the single cross results given in Table 3 were obtained.

Table 3. Values of (d) and (h) with levels of significance, and potence ratios based on individual crosses

Cross	(d)	†	(h)	†	Potence ratio
A × B	28.53	3.73 ^{**}	+ 16.05	n.s.	0.56 ⁽⁺⁾
A × E	27.33	3.72 ^{**}	+ 26.24	2.09 [*]	0.96 <u>≈</u> 1.00
A × F	32.54	4.37 ^{**}	+ 83.00	6.57 ^{**}	<u>2.55</u>
A × H	18.08	2.46 [*]	- 10.90	n.s.	0.60 ⁽⁺⁾
A × M	26.04	3.43 ^{**}	+ 4.12	n.s.	0.16 ⁽⁺⁾
B × E	1.20	n.s.	+ 87.78	6.38 ^{**}	68.98 (++)
B × F	4.01	n.s.	+ 74.16	5.69 ^{**}	18.49 ⁽⁺⁺⁾
B × H	46.61	6.21 ^{**}	+ 20.04	n.s.	0.43 ⁽⁺⁾
B × M	54.57	7.05 ^{**}	+ 32.09	2.45 [*]	<u>5.88</u>
E × F	5.21	n.s.	+121.92	9.47 ^{**}	23.40 ⁽⁺⁺⁾
E × H	45.41	6.28 ^{**}	+ 44.27	3.48 ^{**}	<u>0.97</u> <u>≈</u> 1.00
E × M	53.37	7.15 ^{**}	+ 65.13	5.03 [*]	<u>1.22</u> <u>≈</u> 1.00
F × H	50.63	5.34 ^{**}	+ 76.82	6.12 ^{**}	<u>1.52</u>
F × M	58.59	7.77 ^{**}	+ 73.29	5.64 ^{**}	<u>1.25</u>
H × M	7.96	n.s.	+ 17.82	n.s.	-

(+) Since (h) is not significantly different from zero these ratios may be considered equal to zero.

(++) Since (d) is not significantly different from zero these ratios may be considered equal to infinity, i.e., there are no obvious heterotical conditions.

From Table 3 it is clear that heterosis is quite common for the character plant height. The F₁ progenies of the crosses,

A × F, B × E, B × F, B × M, E × F and F × H, especially, are considerably taller than the tallest parent. Complete dominance is observed in the crosses, A × E, E × H, E × M, and F × M, (in the last two crosses a slight overdominance or heterosis may be assumed). In the crosses, A × B, A × H, A × M and B × H, the dominant deviation is not significantly different from zero. The situation discussed above is graphically illustrated in Fig. 12.

i. Number of internodes

Since the character, plant height, is a function of the number of internodes, the lengths of these, and of the peduncle, are given in Table 4.

Table 4. Average number of internodes (excluding peduncle) per stem per plant and the corresponding variances

	Variety and cross	n_i	\bar{x}_i	s_i^2
1	A	11	5.73	0.4671
2	B	10	5.10	0.3162
3	E	11	4.91	0.6909
4	F	10	5.00	0.2222
5	H	11	5.55	0.2727
6	M	11	5.18	0.5636
7	A × B	10	5.30	0.2333
8	A × E	11	5.36	0.4546
9	A × F	11	5.82	0.1636
10	A × H	11	5.09	0.2909
11	A × M	11	5.09	0.0900
12	B × E	11	5.55	0.2727
13	B × F	11	5.55	0.4727
14	B × H	11	5.27	0.2182
15	B × M	11	5.45	0.3327
16	E × F	11	5.55	0.4727
17	E × H	11	5.18	0.3636
18	E × M	11	5.36	0.2546
19	F × H	11	5.55	0.2727
20	F × M	11	5.64	0.2546
21	H × M	11	5.55	0.2727

n_i = number of plants (one stem per plant) considered
 \bar{x}_i = average number of internodes one stem per plant
 s_i^2 = corresponding variances

The pooled variance is

$$s^2 = \sum n_i s_i^2 / (\sum n_i - k) = 0.3623$$

$i = 1, 2, 3 \dots, k$; $k = 21$ in the present case.

The graphical diallel cross analysis is given in Fig. 13.

Since all W_r , V_r points of intercept are well to the right and below the line of unit slope, heterosis is indicated for all arrays. The position of the W_r , V_r points of the arrays suggest some nonallelic interaction of complementary gene type.

The results obtained for individual crosses are presented in Table 5.

Table 5. Values of (d) and (h) with corresponding t values and potence ratios for each cross

Cross	\pm (d)	t_d	\pm (h)	t_h	Potence ratio
A \times B	- 0.315	2.40*	- 0.115	n.s.	0.36
A \times E	0.410	3.20**	+ 0.040	n.s.	0.10
A \times F	0.365	2.78*	+ 0.455	2.03*	1.25
A \times H	- 0.090	n.s.	- 0.550	2.48*	6.11
A \times M	- 0.275	n.s.	- 0.365	n.s.	-
B \times E	0.095	n.s.	+ 0.545	2.43*	5.74
B \times F	0.050	n.s.	+ 0.500	2.21*	10.00
B \times H	- 0.225	n.s.	- 0.050	n.s.	-
B \times M	0.040	n.s.	+ 0.310	n.s.	-
E \times F	0.045	n.s.	+ 0.595	2.57*	13.23
E \times H	- 0.320	2.49*	- 0.050	n.s.	0.16
E \times M	0.135	n.s.	+ 0.315	n.s.	-
F \times H	0.275	2.09*	+ 0.275	n.s.	1.000
F \times M	0.090	n.s.	+ 0.550	2.45*	6.11
H \times M	0.185	n.s.	+ 0.185	n.s.	-

(*) Significant at 5% level

(**) Significant at 1% level

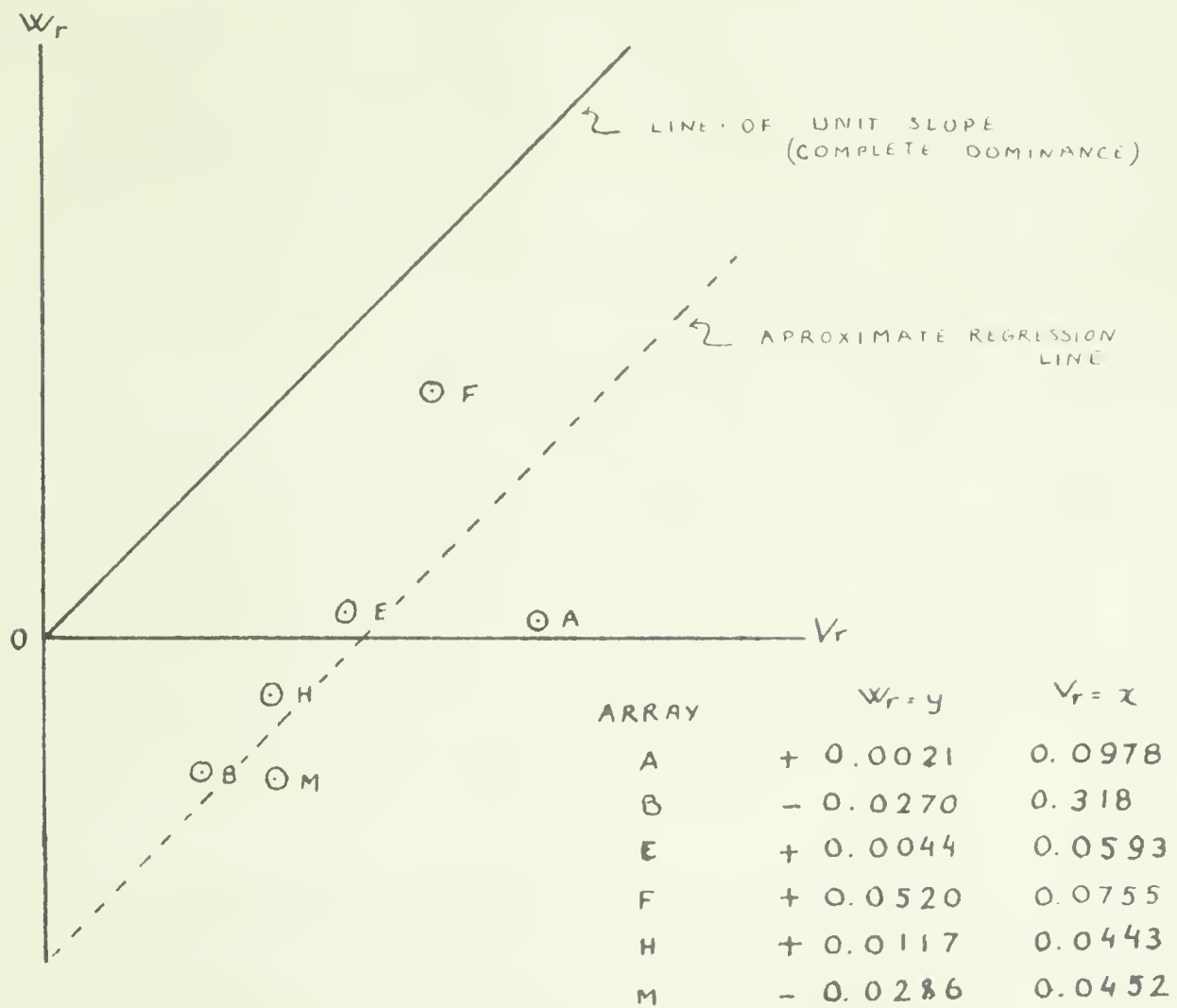


Fig. 13. Number of internodes per plant W_r , V_r graph.

The results show that in the crosses $A \times B$, $A \times E$, $E \times H$ and $F \times H$ the parents are significantly different from each other $[(d) \neq 0]$ but the F_1 generation is not statistically different from the corresponding parental means or mid-parents, i.e. (h) is not significantly different from zero. Consequently, it may be assumed that the genes controlling the character, number of internodes, are acting additively in these crosses.

The cross $A \times F$ shows a slight overdominance $[(d) < (h)]$. Since (d) values are not significantly different from zero, whereas (h) values are, it may be accepted that the crosses $A \times H$, $B \times E$, $B \times F$, $E \times F$ and $F \times M$ manifest a marked heterosis. Finally, the crosses $A \times M$, $B \times F$, $B \times M$, $E \times M$ and $H \times M$ show that the corresponding parental varieties, phenotypically as well as genotypically are more or less alike (non-significant (d) , non-significant (h)).

ii. Length of internodes

The average lengths of the internodes and their weighted means as well as the average length of the peduncle (i.e., the internodes bearing the spike) are given in Table 6. From this Table (d) , (h) and (h/d) values were calculated. The results of the calculations are given in Table 7. The results presented in this Table may be summarized as follows:

(a) Internode I: Pronounced heterosis may be presumed to be present in the crosses $A \times E$, $E \times F$, and $F \times M$ in the direction of the lesser expression of the character, and in the crosses $A \times M$, $B \times M$ and $H \times M$ in the opposite (positive) direction.

Table 6. Internode and pedunculum measurements of individual parents and hybrids

Internodes, mm.														Pedunculum, mm.	
1		2		3		4		5		6		7		Weighted (*)	
\bar{x}_i	n_i	\bar{x}_i	n	\bar{x}_i	n	\bar{x}_i	n_i	\bar{x}_i	n_i	\bar{x}_i	n_i	\bar{x}_i	n_i	mean int.	\bar{x}_i
A	33.00	11	73.76	11	77.73	11	78.91	11	84.27	11	83.33	3	-	70.17	165.91
B	30.50	10	58.50	10	71.50	10	66.20	10	62.30	10	90.00	1	-	58.43	112.00
E	33.18	11	59.54	11	66.36	11	67.50	10	75.22	9	61.50	2	-	59.72	106.36
F	30.00	10	76.50	10	74.50	10	62.00	10	73.33	9	60.00	1	-	63.00	113.50
H	25.45	11	55.91	11	69.55	11	78.64	11	75.64	11	90.00	6	-	63.89	101.18
M	26.82	11	59.05	11	72.91	11	87.54	11	81.67	9	98.75	4	-	67.37	162.73
A x B	33.00	10	78.00	10	91.50	10	81.50	10	84.50	10	96.67	3	-	75.00	124.00
A x E	18.18	11	62.45	11	83.18	11	75.00	11	76.30	10	62.00	5	-	62.71	121.82
A x F	30.91	11	66.82	11	85.91	11	74.55	11	65.91	11	90.00	10	-	68.69	141.82
A x H	31.36	11	70.00	11	79.55	11	86.82	11	91.50	10	86.00	2	-	72.00	132.55
A x M	34.55	11	62.72	11	78.64	11	82.64	11	97.36	11	85.00	1	-	71.43	175.00
B x E	33.45	11	64.54	11	72.00	11	73.18	11	89.09	11	93.33	6	-	69.10	150.45
B x F	30.45	11	64.55	11	71.36	11	68.64	11	82.25	11	81.00	5	60	64.84	112.73
B x H	26.82	11	60.00	11	81.82	11	84.36	11	84.27	11	85.67	3	-	68.40	148.00
B x M	31.82	11	58.18	11	75.00	11	76.82	11	95.91	11	85.00	5	-	65.00	170.18
E x F	25.91	11	58.64	11	68.09	11	93.73	11	88.50	10	96.43	7	-	70.00	181.36
E x H	33.64	11	55.91	11	69.55	11	85.91	11	85.00	10	86.67	3	-	66.75	141.36
E x M	32.05	11	57.27	11	68.36	11	65.00	11	75.91	11	86.25	4	-	61.53	202.27
F x H	28.18	11	60.27	11	72.73	11	97.00	11	91.36	11	84.00	6	-	71.29	171.45
F x M	25.15	11	52.09	11	75.18	11	74.36	11	81.27	11	99.29	7	-	65.92	204.09
H x M	28.64	11	51.82	11	69.09	11	74.82	11	85.91	11	86.17	6	-	64.43	179.09

(*) $W_{mi} = \frac{\sum \bar{x}_i n_i}{\sum n_i} = \frac{\sum x_i}{\sum n_i}$

i = 1, 2, . . . 21

Table 7. Values of (d) and (h) and the (h)/(d) ratio for each hybrid

	Internodes (mm.)																					Average length of internode mm.			Pendunculum mm.		
	1			2			3			4			5			6			7			(d)	(h)	$\frac{(h)}{(d)}$	(d)	(h)	$\frac{(h)}{(d)}$
	(d)	(h)	$\frac{(h)}{(d)}$	(d)	(h)	$\frac{(h)}{(d)}$	(d)	(h)	$\frac{(h)}{(d)}$	(d)	(h)	$\frac{(h)}{(d)}$	(d)	(h)	$\frac{(h)}{(d)}$	(d)	(h)	$\frac{(h)}{(d)}$	(d)	(h)	$\frac{(h)}{(d)}$						
AxB	1.25	1.25	1.00	7.43	12.07	1.62	3.11	16.89	5.43	6.35	8.94	1.41	10.99	11.21	1.02	3.33	10.00	3.00	-	-	-	5.87	10.70	1.82	-26.96	-14.96	0.55
AxE	-0.09	-15.09	167.67	-6.91	-4.00	0.58	5.69	11.14	1.96	5.70	1.79	0.31	-4.52	-3.44	0.76	-10.91	-10.42	0.96	-	-	-	-5.22	-2.24	0.43	-29.77	-14.31	0.48
ExF	-1.50	-0.59	0.39	-1.57	-8.11	5.17	1.61	9.79	6.08	8.45	4.09	0.48	-5.47	-12.89	2.36	11.66	18.33	1.57	-	-	-	3.58	2.10	0.59	26.20	2.11	0.08
AxH	3.77	2.13	0.56	8.72	5.36	0.61	4.09	5.91	1.44	0.13	8.04	61.85	4.31	15.86	3.67	-3.33	-0.66	0.19	-	-	-	3.14	4.97	1.58	32.36	0.99	0.03
AxM	3.09	4.64	1.50	-7.13	-3.50	0.49	2.41	3.32	1.66	-4.31	-0.59	0.14	1.30	14.39	11.06	-7.71	-6.04	0.78	-	-	-	3.40	2.66	0.78	1.59	10.68	6.72
BxE	1.34	1.61	1.20	0.52	5.52	10.61	2.57	3.07	1.19	0.65	6.33	9.74	6.46	20.33	3.15	14.25	17.58	1.23	-	-	-	0.65	10.02	15.41	2.82	41.27	14.63
BxF	0.25	0.20	0.80	-9.00	-2.95	0.33	1.50	1.64	1.09	2.10	4.54	2.16	5.51	14.45	2.62	15.00	6.00	0.40	0*	60.00*	-	2.28	4.12	1.81	0.75	0.05	0.07
BxH	-2.52	-1.16	0.46	1.29	2.79	2.16	0.97	11.29	11.64	6.22	11.94	1.92	6.67	15.30	2.29	0.00	-4.53		-	-	-	2.73	7.24	2.65	5.41	41.41	7.65
BxM	1.84	3.16	1.72	0.30	0.61	2.00	0.70	2.79	3.98	-10.67	-0.05	0.00	9.63	23.97	2.49	-4.37	-8.87	2.03	-	-	-	4.47	6.10	1.36	25.36	32.63	1.29
ExF	-1.59	-5.18	3.26	8.48	-9.38	1.11	-4.07	-1.34	0.33	2.75	28.98	10.54	0.94	14.22	15.13	0.75	35.68	45.57	-	-	-	1.64	8.64	5.27	3.57	71.43	20.01
ExH	3.87	4.32	1.12	-1.81	-1.81	1.00	1.59	1.59	1.00	5.57	12.84	2.31	0.21	9.57	45.57	14.25	10.92	0.77	-	-	-	2.08	4.94	2.37	2.59	37.59	14.51
ExM	3.18	2.09	0.66	-0.22	-2.04	9.27	3.27	-1.27	0.39	-10.02	-12.02	1.20	-3.17	-2.49	0.78	18.62	1.12	0.06	-	-	-	-3.82	-2.21	0.57	28.19	67.72	2.40
FxH	2.27	0.45	0.20	2.48	10.29	4.15	2.47	0.70	0.28	8.32	26.68	3.21	1.16	16.88	14.55	15.00	9.00	0.60	-	-	-	0.44	7.84	17.81	6.16	14.11	2.29
FxM	-1.59	-2.96	1.86	-8.70	-15.70	1.80	0.79	1.47	1.86	-12.77	-0.41	0.03	4.17	3.78	0.91	19.37	19.91	1.03	-	-	-	2.18	0.74	0.34	24.61	65.97	2.68
HxM	0.68	2.50	3.67	-1.59	-5.68	3.50	-1.68	-2.14	1.27	-4.45	-8.27	1.86	3.01	7.25	2.41	-4.47	-8.20	1.83	-	-	-	-1.74	-1.20	0.69	30.77	47.14	1.53

* The only case where seven internodes were recorded.

(b) Internode 2: Heterosis in the negative direction (i.e., toward the lesser expression of the character) is present in the crosses $A \times F$, $E \times M$, $F \times M$ and $H \times M$, and in the positive (i.e., toward the higher expression of the character) in the cross $A \times B$, $B \times E$, $B \times H$ and $F \times H$.

(c) Internode 3: Heterosis is present in the positive direction only; crosses, $A \times B$, $A \times E$, $A \times F$, $B \times H$, $B \times M$ and $F \times M$.

(d) Internode 4: Heterosis in the positive direction only in the crosses $A \times B$, $A \times H$, $B \times E$, $B \times F$, $B \times H$, $E \times F$, $E \times H$, $F \times H$ and $H \times M$ (i.e., in nine out of fifteen crosses).

(e) Internode 5: Heterosis in the positive direction in the crosses, $A \times H$, $A \times M$, $B \times E$, $B \times F$, $B \times H$, $B \times M$, $E \times F$, $E \times H$, $F \times H$ and $H \times M$, and in the negative direction in the cross, $A \times F$.

(f) Internode 6: Heterosis in the positive direction in the crosses $A \times B$, $A \times F$, $B \times E$ and $E \times F$, and in the negative direction in the crosses $B \times H$, $B \times M$ and $H \times M$.

(g) Internode 7: The only case of seven internodes was observed in the progeny of the cross, $B \times F$, and in only one plant.

(h) Average length of the internodes: Heterosis is present in the crosses $A \times B$, $A \times H$, $B \times E$, $B \times F$, $B \times H$, $B \times M$, $E \times F$, $E \times H$ and $F \times H$. In all cases its direction is positive, i.e., toward the higher expression of the character.

iii. Length of pedunculum

Regarding this character, there is positive heterosis in most of the crosses, namely, $A \times M$, $B \times E$, $B \times H$, $E \times F$, $E \times H$, $E \times M$, $F \times H$, $F \times M$ and $H \times M$ (i.e., in nine out of fifteen crosses).



In conclusion it may be said that heterosis observed for plant height may express itself in the number of internodes, their length and in the length of pedunculi. This expression may be of a reinforcing kind, as in the $F \times H$ cross, or of an opposing kind, as in the $A \times M$ cross. This latter cross, in spite of marked heterotic effects in some or all subcharacters, may not show heterosis, or even dominance, for the character plant height.

V. DISCUSSION AND CONCLUSIONS

It may be accepted that heterotic effects have to be considered in both positive and negative directions.

From the different counts of tillers, it was observed in most of the hybrids that the character, number of tillers per plant, shows positive heterosis during the first forty-five days of development and negative heterosis at the time of flowering and at maturity. This means that the hybrids distinguish themselves by a more rapid and shorter period of tiller formation, as compared to the corresponding parents.

The character, days-to-heading, demonstrates quite clearly the presence of negative heterosis; especially in the hybrids of the crosses $B \times E$, $B \times F$ and $B \times H$. Since (although less pronounced) this situation is true for the most of the hybrids considered, it may be concluded that at least under the environmental conditions in which the present investigation was conducted, earliness tends to be inherited as a dominant, and often as an overdominant (heterotic), trait.

The character, days-to-flowering, is quite similar to that of days-to-heading regarding its inheritance. This suggests that these characters are controlled by the same set of genes or by closely linked genes.

Regarding the character, top weight (i.e., the amount of organic mass per plant produced above the soil level) eleven hybrids, out of fifteen, exhibit heterosis to a significant degree, its direction being toward the higher expression of the character.

Although the situation regarding the character, root weight per plant, appears more or less similar to that for the top weight, more detailed analysis shows that, contrary to top weight, the heterotic transgressions are mainly in the direction of lower expression of the character. The first impression would be that there is a rather paradoxical situation in which higher top weights per plant are associated with lower root-weights per plant. However, although there is a pronounced negative correlation between the potence ratios (Fig. 9), the correlation between the actual root weights and top weights is $\pm r_{+w/rw} = + 0.700$ for the parents and $\pm r_{tw/rw} = + 0.615$ for the crosses (4 and 13 d.f., respectively). This means that, although in some instances high top weight may be associated with a rather low root weight, as a general rule similar expressions of both characters would coincide.

The graphical treatment of the 6-parent diallel set shows that, respecting the character, spike (rachis) length, there is on the average complete dominance. This does not, of course, exclude



the possibility of transgressions in single hybrids within the arrays. Such transgressions are shown by the hybrids, B x E, B x H, B x M, E x F and F x H, the direction of the heterosis being toward the lower expression of the character.

The character, grain yield, is inherited as a dominant and, in the present case, more often as a transgressive trait, the direction of the dominance deviation being toward the higher expression of the character.

The character, plant height, may be considered individually or as a function of the subcharacters (i.e. number of internodes per stem, length of internodes and the length of the pedunculum). Plant height as a resultant of the subcharacter effects appears, on the average, as an overdominant trait with only a slight suggestion of the presence of nonallelic interaction (Fig. 12, array E). However, more detailed analysis shows that heterosis is not present in all hybrids (Table 3). Although the resultant effect (plant height) is unidirectionally toward the higher expression of the character, the effects of subcharacters are not. For instance, for number of internodes the direction of heterosis in the hybrid A x H is toward the lower expression of this trait. The same is generally true regarding the remaining subcharacters.



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